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SOME HABITS AND SENSORY ADAPTATIONS OF CAVE-INHABITING BATS. II.

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PAGE.

Experimental Studies.

1. *Avoidance of Objects.*

As early as 1794 Spallanzani experimented with bats in which one or more of the senses had been destroyed. I have not had access to the original account of his experiments. According to the account of these experiments given by Godman ('26) and Flower and Lydekker ('91), bats deprived of sight, hearing and

smell, were able to avoid objects in their way and even silken threads stretched so that there was just room for the animals to pass between, and they contracted the wings when the space was too narrow for the expanded wings to pass through. Observations on a large number of captive bats have convinced me that Spallanzani's experiments were, in some way, lacking in scientific accuracy. Not a single individual out of more than sixty belonging to five species that I have experimented with, have shown any approach to this degree of skill in avoiding objects, even with the senses all intact.

The experiments here described were made at the "University Farm" in the spring and summer of 1907, and were checked by additional ones in the laboratory of Indiana University in December of the same year. They were similar in part to those made by Rollinat and Trouessart ('00), with, however, a simpler arrangement of obstacles and with each experiment worked out quantitatively.

The experiments show that bats are able to avoid objects when flying, but that avoidance is not complete. Several senses may be of use in perceiving obstacles, and air currents perhaps guide the animals to some extent. However, destruction of the sense of sight does not seriously impair their ability to perceive objects nor does the loss of the external ears and tragi. The most important senses are located in the internal ear and any disturbance of these organs seriously impairs the animal's ability to perceive and avoid obstacles.

The following method was used: The bats were liberated in an unceiled room approximately fifteen feet wide, eighteen feet long, nine feet from floor to eaves and twelve feet from floor to the apex of the roof. Pieces of black, annealed iron wire about one millimeter in diameter were suspended from the rafters and kept moderately tight by fastening the lower ends to a cross wire five feet from the floor. On an average, there was one wire to each eleven inches of space, but they were spaced unequally, the purpose being to determine whether the bats would try to pass through the more narrow spaces or learn to select the wider ones. During a part of the experiments there was an additional row of seven short wires alternating with the others and placed twenty inches from

the first row, but they were high in the comb of the roof, the bats seldom passed between them, and as they had no apparent effect upon the experiments they will be counted as though all were in one series.

Wires were used in these experiments in preference to larger objects because a bat will invariably try to perch on any object it strikes and it is sometimes difficult to tell whether the animal intended to perch or whether it did not perceive the object. Wires have an advantage over strings because the slightest touch causes a perceptible sound and it is not always easy to *see* whether an object is touched. Some preliminary experiments were made in April but the method of quantitative study was not decided upon until May 16, when one bat was used. Several more were tried during May and June but at this time few bats were in the cave. The experiments were therefore discontinued until later and most of them were made between August 25 and September 5.

Some of the animals were very fat and inactive during late summer and it was difficult to keep them flying. There are great individual differences and some of the experiments required six times as long as others and some bats had to be discarded for the purpose of these experiments because they would not fly at all or would make short flights in one corner of the room and not attempt to pass between the wires. The tabulated results were obtained from the use of 48 bats belonging to three species. About fifteen additional individuals and two additional species were liberated in the experiment room but are omitted from the tables because the data are incomplete. The total number of observations on avoidance is about 6,000.

The individual differences and the varying degrees of lethargy in the same individual at different times make it essential to determine the normal reactions of each animal before trying experiments under changed conditions. For this reason it was deemed necessary to test each individual in a normal and uninjured condition immediately before the experiment in which one of the senses was impaired.

The bats were captured in the cave and were generally used for the experiment on the same day, although some of them were

not used until the next day. The normal, uninjured animals were liberated in the room and their movements carefully watched. Each time one of them passed between the wires or approached quite near to a wire and appeared to dodge it was called a trial. It was at first intended to allow 100 trials for each bat but it was found that the animals were apt to become tired and refuse to fly before the experiment was concluded and the number of trials was reduced to 50 for each condition. The wings brushing against the wires, even very lightly, produce an audible sound so that it was easy to tell when the animal struck the wires.

Most of the normal bats flew about the room rapidly for a time and then began to stop frequently, alighting on the walls, the underside of the roof or objects in the room. After a period of varying length some of them attempted to settle down and it was difficult to keep them on the wing. On being driven from their perch they would make short flights only, and stop again. For reasons previously stated (p. 167) striking objects other than the wires were disregarded.

Four kinds of mutilation were employed: (1) The eyes were covered with an opaque mixture of lamp black and glue. (2) The external ears and tragi were excised close to the head. (3) The external auditory meatus was stopped with a small quantity of plaster of Paris which was allowed to harden before the bat was liberated. (4) The hairs of the body and membranes were pasted down with thick vaseline.

When the eyes were covered with the mixture of lamp black and glue, the most noticeable effect was to decrease the activity of the animal. Usually a bat so treated alights somewhere and tries to remove the substance from its eyes, using the hind foot, as the thumb and wrist cannot be brought into contact with the head. If the glue is allowed to harden somewhat before the animal is liberated, it is not so easily removed; even then it is necessary to dislodge the bat as soon as it alights or it will finally succeed in removing the hardened glue. In every instance the animals were examined at the conclusion of the experiment to see that the covering was intact.

The 47 bats used in these experiments struck the wires 25 per cent. of the 2,350 trials recorded for the uninjured condition.

Twelve of the forty-seven were blinded in the manner previously described and given fifty trials each. In these 600 trials the percentage of hits was 21.7. However, the percentage of hits for the same twelve in the normal condition was only 23.6 per cent. as compared with 25 per cent. for the total forty-seven.

TABLE I.

AVOIDANCE OF WIRES.

Myotis lucifugus.

No. of Bat.	Condition Normal.		Eyes Covered.		Ears and Tragi Excised.		Meatus Stopped.		Hair Covered.	
	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.
1	3	8	3	3					7[1]	2
2	9	5	6	6					5[1]	15
3	8	4	1	4			16	21		
4	15	6					19	13	9[2]	8
5	8	7					17	17		
6	8	7					17	18		
7	9	6					18	14		
8	1	3					16	15		
9	8	6			9	5				
10	6	6			15	12				
11	7	5			5					
12	6	3			5	7				
13	8	6			9[3]	5			7	4
14	8	6							15	20
15	7	4								
16	5	3								
Average No.	$7\frac{1}{16}$	$5\frac{5}{16}$	$3\frac{1}{3}$	$4\frac{1}{3}$	$8\frac{3}{5}$	$7\frac{1}{4}$	$17\frac{1}{6}$	$16\frac{2}{6}$	$8\frac{3}{5}$	$9\frac{4}{5}$
Total per cent.		24		15.3		31.4		66.6		36.4

It is therefore apparent that bats deprived of the sense of sight not only are able to avoid objects but, in these experiments, they avoided them better while blinded than they did with sight unimpaired. This does not necessarily mean that they perceived objects more readily with the eyes covered. It was noted that there was a greater tendency to avoid the vicinity of the wires when blinded. The flight seemed slower, although it could not be measured, and more care was probably used to avoid objects.

[1] Eyes freed. [2] Meatus freed. [3] Hair covered first.

The second condition of these experiments, the removal of the ears is also without marked effect on the perception of objects. Five *M. lucifugus* struck the wires 31.7 per cent. of the chances as against 24.4 for the same individuals when normal, and 25 per cent. for all individuals used. Six *M. subulatus* struck 24.6 per cent. of their chances with the ears and tragi removed as against 32.6 per cent. for the same animals when normal. Four *P. subflavus* struck 20.8 per cent. when operated upon and 26 per cent. when normal.

The high percentage of strikes for *M. lucifugus* after the operation is due to a single individual which was injured in the operation. When it is omitted, the percentage for the other four is 24.3, or about that for the normal individuals. The average per cent. for all three species is 23.2 or 1.8 per cent. less than the total average. This difference is so small that it may be accidental and without significance. However, this set of experiments shows that the external ears and tragi are not necessary for the perception of objects. These results are in accordance with the conclusions reached by Rollinat and Trouessart ('00) and Merzbacher ('03).

To stop the external auditory meatus dry plaster of Paris was pressed in lightly with a pair of forceps, and then wet with a drop or two of water. The superfluous water and plaster was wiped out of the ear conch and the bat was held firmly for a few minutes until the mixture hardened. Even then the animals would break the hardened plaster from the ear if they were allowed to rest very long. They were examined at intervals and no trials were recorded in which there was a possibility of the plaster having been removed.

The results were very different from those obtained from the previous experiments. Six *M. lucifugus* struck the wires 67 per cent. of the chances. The same six in the normal condition struck but 26.3 per cent. Five *M. subulatus* struck 65.2 per cent. of chances with ears stopped and the same five normal struck 26 per cent. Five *Pipistrellus subflavus* struck 65.6 times and only 23.2 when normal. The concordance of the figures for these experiments, divided into three groups, is significant and shows that the results are not due to accident but have some common basis.

There are, however, complicating factors which make the interpretation of the results somewhat difficult since the exact way in which the ears are affected is not known. A male *M. lucifugus* used on July 15 seemed to be able to equilibrate perfectly but it flew with a heavy, uncertain flight and was never observed to dodge an object. When it came in contact with any object to which it could secure hold with its claws it clung to it, but always alighted in the position in which it happened to strike instead of reversing in the air and alighting head down. Another bat was able to right itself when tossed end over end into the air but it was never seen to dodge and it struck the wires on 66 per cent. of the trials. Others acted in a similar manner.

Table II.

Avoidance of Wires.

Myotis subulatus.

No. of Bat.	Condition Normal.		Eyes Covered.		Ears and Tragi Excised.		Meatus Stopped.		Hair Covered.	
	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.
1	5	7					18	20		
2	6	6					16	17		
3	5	11					17	15		
4	9	7					19	16		
5	5	4			1	7	17	8[2]		
6	7	5			9	9[1]			5	9
7	7	5			6	4			14	14[2]
8	6	4			7	5			9	7[2]
9	8	4			8	6			11	12[2]
10	7	8	6	6					7	11
11	9	7	10	6						
12	6	7	8	10						
13	6	5	9	8	5	9				
14	6	6								
Average No.	$6\frac{6}{14}$	$6\frac{2}{14}$	$8\frac{1}{4}$	$7\frac{2}{4}$	6	$6\frac{4}{6}$	$17\frac{2}{5}$	$15\frac{1}{5}$	$9\frac{1}{5}$	$10\frac{3}{5}$
Average per cent.		25.1		31.5		24.6		65.2		39.6

It is difficult to calculate exactly the number of probable strikes if there were no avoidance because the wires were unequally spaced and because the distance between the tip of the wings is

[1] Hair covered.

[2] Ears and tragi removed first.

less on the up and down stroke than when horizontal. The average expanse of the two species of *Myotis* is ten inches. If we deduct one inch for the contracted wings and assume the wires to be equally spaced, the probable percentage of hits is 82. There is therefore some avoidance even when the ears are stopped.

The fact that bats with the meatus plugged were able to equilibrate and alight on objects which they struck would seem to indicate that the disturbance was not a mechanical one, *i. e.*, due to the weight of the plaster or to sensations caused by its pressure on the tympanum or labyrinth, but that it was due wholly to an interference with sensation, and probably to the failure of vibrations to reach the sensory cells of the internal ear.

Table III.

Avoidance of Wires.

Pipistrellus subflavus.

No. of Bat.	Condition Normal.		Eyes Covered.		Ears and Tragi Excised.		Meatus Stopped.		Hair Covered.	
	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.
1	5	7					23	19		
2	9	9					17	17		
3	3	6					15	18		
4	6	7					16	15		
5	2	4	2	2			16[2]	17	7[1]	4
6	5	2	5	7					8[2]	9
7	6	4	4	3						
8	7	4	7	4						
9	8	5	6	5					9[2]	5
10	11	13							10	15
11	7	6							8	7
12	8	11			4	8				
13	9	4			5	7				
14	6	7			6					
15	5	2			4	2				
16	3	6			12	11				
17	7	2								
18	5	12								
Average No.	$6\frac{2}{9}$	$6\frac{3}{18}$	$4\frac{4}{5}$	$5\frac{1}{5}$	$6\frac{1}{5}$	7	$15\frac{2}{5}$	$17\frac{2}{5}$	$8\frac{2}{5}$	8
Average per cent.		24.4		20		26.4		65.6		32.8

[1] Eyes and ears freed.

[2] Eyes freed.

Hearing undoubtedly aids the bat to secure the flying insects on which it feeds and thus has been developed to a high degree by natural selection. The perception of a stationary object is probably due to the condensation of the air between the flying bat and the solid body that it is approaching. If hearing is relatively as well developed in a bat as smell is in a dog it is not difficult to imagine that condensation of the air so slight as to be imperceptible to the human ear will arouse sensations on the auditory end organs of the bat. It is reasonably certain that the highly modified external auditory apparatus of a bat has some important function, the exact nature of which is unknown. Flower and Lydekker ('91) state that the function of the tragus is probably to "cause undulations in the waves of sound and so intensify and prolong them." As far as I am aware, no attempt has ever been made to more definitely define the function of that organ. It seems to me highly probable that it also has a selective action, perhaps destroying waves of certain kinds and intensifying others.

It is necessary to bear in mind in discussing the senses of the lower animals that it is impossible to form any adequate conception of the sensations and mental life of the lower animals on the basis of our own. If a piano recital is incomprehensible to a Hottentot, or a snake dance to a cultured Caucasian, how much less can either hope to understand the perceptions aroused in the brain of a hound that scents a fox, or the mental processes of a bat as he circles among the tree tops in pursuit of insects?

The body of a bat is covered with fine hairs of a peculiar structure. The membranes also support hairs, the number varying considerably in the different species. These hairs are supposed to have a sensory function. No means was devised for completely destroying the sense organs located in them without seriously injuring the animals. But they were coated with thick vaseline which pasted the hairs together and made them less sensitive to slight stimulation.

The experiments under these conditions yielded the following results: Five examples of *M. lucifugus* with the hair so coated struck 36.4 per cent. of chances. The same five normal struck 28.8 per cent. Five *M. subulatus* struck 39.6 per cent. of trials

with the hair covered, and 24.4 per cent. when normal. For five *P. subflavus* the proportions were 32.4 per cent. and 25.2 per cent.

The difference of proportion for these three species is considerable and there is no reason apparent. It is not safe, however, to infer that there is any important difference in the sensibility of the hairs of these species for there is a large individual variation, both the lowest and highest individual percentages being found in *Myotis lucifugus.*

The figures indicate that the organs of touch, located in the skin and probably associated with the hairs, are of value in enabling the animals to avoid objects, though of lesser value than the auditory organs. However, it is necessary to take into consideration the mechanical effect of the vaseline in making the wing membranes sticky. Invariably the flight of the bat became more labored, it stopped more frequently and was less readily dislodged from its perch after being covered with the vaseline, although the animals were able to equilibrate and alight on either vertical or horizontal surfaces as well as when in the normal condition.

In order to check the experiments made at the "University Farm" and to determine some points that were overlooked, additional experiments were made in the laboratory at Bloomington, in December, 1907. In place of the wires spaced at irregular intervals, white cotton tapes, 15 millimeters in width, were stretched from floor to ceiling and spaced regularly, the distance between them being 12 inches. The average expanse of *Myotis lucifugus* is 10 inches and there was thus an allowance for error of 2 inches, supposing the bats aimed at the middle of the space. However, the percentage of hits for five individuals, of *M. lucifugus* in 50 trials each was 58.4 when normal and 60 with the eyes covered, as against an average of 25 per cent. in the earlier experiments.

This discrepancy can perhaps be accounted for in part by the method of counting hits. When the wires were used the hits were counted only when audible. With the tapes it was necessary to adopt some other method of counting and a "hit" was recorded every time that the moderately loose tapes were set in motion by

the animal. This could happen without actual contact with the tapes. However, it is improbable that this difference in method alone would account for so great a difference in results. The greater rigidity of the wires would doubtless make them easier to distinguish if the air condensing theory be correct, but not if sight were relied on. The bats would also have less cause to avoid the tapes because striking them would cause no pain. In this set of experiments a distinction was made between "hits" in which the animal struck the tape squarely with the body or upper part of the arm, and "touches" in which the obstruction was merely brushed with the tip of the wing. The preponderance of the latter bears out the assumption that no attempt was made to avoid the objects.

In these experiments each set of fifty trials was divided into five groups of ten each, the object being to see whether there was a progressive decrease of the percentage of hits due to experience. An examination of the table shows that there is no progressive decrease either in the "hits" or "touches," nor for the normal or blinded condition.

Table IV.

Avoidance of Tapes.

Number of Bat.		Condition Normal.					Eyes Covered.				
		1st 10 Trials.	2d 10 Trials.	3d 10 Trials.	4th 10 Trials.	5th 10 Trials.	1st 10 Trials.	2d 10 Trials.	3d 10 Trials.	4th 10 Trials.	5th 10 Trials.
1	Touches.	6	5	9	3	6	6	4	5	5	6
	Hits.	1	2	1	2	6	2	4	0	3	2
2	Touches.	5	7	5	4	2	5	3	2	2	2
	Hits.	3	0	0	2	0	0	1	1	2	2
3	Touches.	6	7	3	3	9	4	3	2	7	4
	Hits.	0	1	2	2	0	2	1	2	0	2
4	Touches.	6	7	5	7	4	7	9	10	8	9
	Hits.	1	1	1	0	0	0	0	0	1	0
5	Touches.	3	2	2	3	2	6	3	1	5	4
	Hits.	1	2	1	1	1	1	2	0	0	0
Average No. of Touches.		$5\frac{1}{5}$	$5\frac{3}{5}$	$4\frac{4}{5}$	4	$4\frac{3}{5}$	$5\frac{3}{5}$	$4\frac{2}{5}$		$5\frac{2}{5}$	5
Average No. of Hits.		$1\frac{1}{5}$	$1\frac{1}{5}$	1	$1\frac{2}{5}$	$1\frac{2}{5}$	1	$1\frac{3}{5}$	$4\frac{3}{5}$	$1\frac{1}{5}$	$1\frac{1}{5}$
Average of both.		$6\frac{2}{5}$	$6\frac{4}{5}$	$5\frac{4}{5}$	$5\frac{2}{5}$	6	$6\frac{3}{5}$	6	$4\frac{3}{5}$	$6\frac{3}{5}$	$6\frac{1}{5}$

Per cent. of totals for normal condition, 60.8.

Per cent. of totals for blinded condition, 60.

To determine whether there was any avoidance or whether the animals hit or missed by accident, a ball of cotton with one diameter equal to the expanse of the bat and the other slightly smaller, to compensate for the upward stroke of the bat's wing when the distance from tip to tip is somewhat less, was thrown at random at the tapes. The ball struck 82 per cent. of the trials, or approximately the calculated number, as against the maximum of 60 per cent. for the bats.

The difference is more apparent when we separate the "hits" from the "touches." For the ball the "hits" were 48 per cent. of the total chances and "touches" were 34 per cent. For the animals the percentage of "touches" in the normal condition is 48.4 and 49 with sight eliminated. On the other hand, the "hits" were 9.6 per cent. of the chances under normal conditions and 16.6 per cent. with the eyes covered. From these figures it is apparent that the animals avoid striking objects in such a way as to impede their flight much more often than they avoid brushing against them with the tips of the wings.

In the caves I have often seen horizontal scratches on mud banks or on slime-covered walls that must have been made by flying bats that were unable to completely avoid the obstacles in their path. I have not seen any evidence that they ever strike the walls hard enough to do themselves injury. The great agility with which a bat can check its flight or change its course enables it to either turn aside or take hold of an object which it strikes even if it is not perceived until the animal is almost against it. It is highly probable that the fatty pads which lie about the nostrils have a protective value and prevent injury to the animal when it strikes, head on.

The experiments described above show that bats do not always avoid obstacles in their path. Spallanzani's statement as to the accuracy with which they perceive objects in their pathway, on which a number of writers on natural history have based erroneous statements, are incorrect, at least in so far as they apply to the species studied in the preparation of this paper. On the other hand, these experiments show that bats do perceive objects that they are approaching by senses other than sight or hearing as usually understood. The most important sense organs for the

perception of objects are in the internal ear. The hairs of the body and membranes also have a sensory function. The external ears, the tragi and the eyes are not necessary for the guidance of the animals, although there is reason to believe that when they are flying in the light they depend, to some extent, upon the sense of sight to perceive objects.

Additional Observations.

A large brown bat, *Eptesicus fuscus*, brought into the experiment room May 2 seemed wholly unable to avoid the wires. It flew rapidly, was not seen to dodge any obstacle, and struck the wires 67 times out of 100 chances when uninjured. It appeared to be frightened by its unusual surroundings.

A long eared bat, *Corynorhinus macrotis*, captured May 1, struck 52 times out of 102 chances. After it had been flying in the room for ten or fifteen minutes it began flying against the windows. It returned to the same point time and again, striking the pane when the window was closed or the wire screen, if the window was open. Usually it struck with considerable force and fell to the sill, but immediately got up and repeated the performance. An adult *Myotis lucifugus* liberated in the house on April 30 acted in the same way and other individuals of both the common species of *Myotis* flew against the glass and window screen.

There were great and unaccountable individual differences in this regard. A male *M. subulatus* on September 3 struck the screen repeatedly, both when the eyes were normal and when they were blindfolded. Another male of the same species used on the following day flew directly toward the screen a number of times but always turned in time to avoid it. Apparently in these instances the animals were depending upon the sense of sight in guiding their movements. The window glass would be invisible to an animal that had never had experience with transparent objects and the wire screen was not very apparent against the background of trees among which the house is situated. The actions of the bats in flying about the room at certain times seemed to indicate that they were depending on sight for guidance in avoiding the wires. The flight when the eyes were cov-

ered was usually slower and more cautious than when the senses were unimpaired.

In the cases where they flew against the screen that obstructed the open window, the bats may have been attracted by incoming currents of air. In experimenting with them in a closed room they almost invariably found the cracks under doors, in the sides of the room, or under the roof and the experiments were seriously delayed by a large number of the animals escaping through crevices which were overlooked or were supposed to be too small for the passage of their bodies. They always explore every corner of any compartment into which they are placed and their manner often indicates that they are attracted to an opening from a distance of several feet when the air currents are the apparent stimulus.

II. *The Formation of Associations and the Sense of Direction.*

The experiments described in this section deal chiefly with a single kind of association, namely, that of place. In studying this sort of association, data were obtained which seem to indicate the presence of a sense of direction not based directly on any of the five senses commonly recognized.

The peculiar habits of a bat make it impossible to employ the methods generally used by animal psychologists in studying the formation of associations. Bats will not go to a dish for food at regular intervals. Although they readily learn to escape from any possible opening, they do not have any adaptation for grasping which would enable them to learn to pull a string or raise a latch and so open a door.

I did not find any evidence that associations of form or color are ever formed. Such associations are hardly to be expected in animals with visual organs so poorly developed.

Sound associations are formed readily. A sucking noise made by the lips at first alarmed the animals, but they soon learned to associate it with feeding. On hearing it they would look about and snap at any object that could be mistaken for food. One individual (bat No. 2 mentioned below) was especially quick to form this association and learned to come on hearing the sound, although it did not learn to localize it definitely. Alcock ('99)

states that a hairy-armed bat, *Vesperugo leisleri* (*Pterygistes leisleri*), learned to come for food on hearing a pair of scissors clicked together.

For studying place associations the following method was used: The bats were kept in cages in the dark room as previously described. For the experiments they were taken into a well lighted room and placed in a small experimental cage made of wire cloth, the sides being of one fourth inch mesh and the top, bottom and ends of one eighth inch mesh. The dimensions were 12 by 13 by 27 inches. On one side was cut a hole seven inches square. This opening was closed with a door made of the same material as the side, and overlapping the edges an inch all around. It was fastened with a wooden latch on the outside. A piece of white cloth, three inches square, was fastened inside the cage, near the upper left corner of the door.

The bat to be used in the experiment was placed on the floor of the cage near the middle. All of its movements were carefully recorded during the whole time it was in the cage. As soon as it touched the cloth while following its natural tendency to explore every part of the cage, the door was opened and a meal worm was offered it with a pair of forceps.

Animals that had never been handled were usually frightened away by thrusting the hand toward them and moreover they did not know how to eat the meal worms. Therefore it was necessary to use bats that had been in captivity for some time and had learned to eat the food offered them.

As soon as the animal under observation had eaten the food given it, it was again placed on the bottom of the cage and given another chance to come to the same place for a worm. The time required was carefully noted and also the movements of the animal which did not result in bringing it nearer to the food.

The curves given by Porter ('04) for similar observations on English sparrows, and Kinnaman ('02) for monkeys, are fairly uniform after the animal had found the food once or twice. The animals used by these observers apparently responded in about the same way to the same stimulus in all instances where there was no disturbing factor. The reactions of a bat are much less constant. When placed in the experimental cage it sometimes

goes at once to the spot where food is given. At other times when it should be about as hungry, it sits quietly on the floor for five minutes or longer and then goes without error or hesitation for the food. Even when it wanders about the cage instead of going directly to the feeding place, it cannot be asserted that the animal has forgotten where it must go for food; the impulse to explore the cage may be stronger than the hunger impulse.

The erratic behavior of bats makes it impossible to tabulate the results or to plot a curve of the time of response that will give a correct idea of the behavior of the animal. For this reason the record of the observations for one bat will first be given in considerable detail, and the conclusions will be stated afterward.

This bat, a female *Myotis subulatus*, recorded as No. 2 in my experiments, was obtained in Shawnee Cave at Mitchell on December 8, 1907. It was kept in a small cage with other bats in the dark room and was occasionally taken out and fed meal worms and allowed to fly about the laboratory. It could always be easily aroused from its dormant state and was unusually alert and active.

In the following records it is to be understood, unless otherwise stated, that the time recorded is that from the instant the animal was released in the middle of the cage until it touched the cloth.

This bat was first placed in the experimental cage on February 7, at 2:06 p. m. (1) It ran and flew about in all parts of the cage and in three minutes reached the cloth and took it in its teeth, probably mistaking it for food because it moved when touched. (2) Was fed and remained quiet for a time, then left and came back and was fed at 2:27. (3) Put on bottom of cage and came back in 1½ minutes but left before it could be fed. (4) Back and fed 3 minutes later. Crawled away and became quiet and was taken out.

Was not put in again till February 10, at 3:39. First time came to cloth in 6 minutes; second time in 1½; third in 1; fourth in 2; fifth in 70 seconds; then in 40 seconds. Experiment terminated.

It is evident that the association had been definitely formed at this time or after a total of ten trials, the first four of which occurred three days earlier than the last six.

February 11: (1) Put on floor of cage at 3:25. Flew up to cloth in 20 seconds. (2) Flew up to front, went across to cloth and began pulling at it in 17 seconds. (3) Flew directly to cloth after ten seconds. (4) Looked about, flew to right end of front, then ran to cloth in 30 seconds. (5) Hesitated and looked about, then flew to front and reached cloth in 30 seconds. (6) Was quiet, then turned and flew directly to cloth in 40 seconds. (7) Went to corner of cage, hesitated, then flew to front and went directly to cloth in 35 seconds. (8) Flew directly to cloth in 10 seconds. (9) Did not move for 75 seconds, then turned partly around and flew directly to cloth. (10) Looked around, scratched itself and washed its face, then after 2½ minutes, flew without hesitation to cloth.

Was not taken out of the living cage on February 12.

February 13: (1) Put in cage at 3:58½. Flew to end of cage and climbed across to cloth in one minute. (2) Flew to right front, walked across and was fed in 20 seconds. (3) Looked around and flew directly to cloth in 12 seconds. (4) Turned around several times, flew into corner and went to cloth in 45 seconds. (5) Was quiet an instant, turned and flew to cloth in 45 seconds. (6) Put on floor, flew to front of cage near cloth, turned toward it but stopped, looked about, then cleaned its fur and became quiet; nearly five minutes after being put on the floor it again began to look about, then went directly to cloth and was fed. (7) At once ran to front of cage and climbed it but did not go to cloth till 3 minutes later. (8) Remained quiet a minute, then climbed up in corner nearest cloth and rested a minute, then went directly to cloth. (9) Remained quiet on floor for a minute, then flew to end of cage and remained for some time, when the experiment was discontinued.

February 14: There were no peculiarities in its activity. The times for the trials were as follows: (1) 15 seconds; (2) 20 seconds; (3) 10 seconds; (4) 7 seconds; (5) 20 seconds; (6) 30 seconds; (7) 12 seconds; (8) 45 seconds; (9) 45 seconds; (10) failure, the animal settled at one end of the cage and remained there until taken out.

Was not put in the experimental cage nor fed on the fifteenth, sixteenth, or seventeenth.

February 18: (1) Put in at 2:47 and flew about the cage, bumping the sides; rested on the bottom, then flew to front and went to cloth in 4½ minutes. (2) Put on floor, rested on end of cage, then went to cloth in 6¼ minutes. (3) Flew to front and went across to cloth in 20 seconds. (4) Flew to door of cage in 10 seconds, but seemed to have learned that food came in through door and waited there. Got to cloth in one minute. (5) Sat on floor without moving for 2 minutes, then flew directly to cloth but started across to edge of door before it could be fed. (6) Was quiet 1 minute, then flew directly to front of cage and reached cloth in 70 seconds but again turned to door. Was put back on floor without being fed, started away but came back and began chewing cloth and was fed 2½ minutes after being first put on the floor. (7) Remained quiet 3 minutes, then flew to front and started toward cloth but stopped and cleaned its fur, remaining there 15 minutes; then turned suddenly and went directly to cloth. (8) Remained quiet 1 minute, then flew directly to cloth. (9) Remained on floor for 10 minutes and then was taken out.

February 19: (1) Put in at 2:05, seemed rather torpid; walked across cage, then remained quiet until 2:13 when it flew directly to cloth. (2) Flew to front of cage and started to cloth in 45 seconds but stopped, 20 seconds later went to it but heard my hand at door and started to it; was not fed; 1 minute later, turned and went again to cloth and was fed. (3) Remained quiet, then flew to front and went directly to cloth and pulled at it with its teeth in 2½ minutes. (4) Was quiet, then flew directly to front and went to cloth in 1 minute. Was beginning to turn toward door again when fed. (5) Cleaned its fur and was quiet, then flew directly to cloth in 4½ minutes. (6) Was quiet, then flew directly to cloth after 7 minutes. (7) Quiet, flew directly to cloth after 3 minutes. (8) Quiet, flew directly to cloth after 2 minutes. (9) Quiet, flew to front and went directly to cloth in 1¾ minutes. (10) Quiet, flew to front near cloth in 2 minutes, but remained there cleaning fur 6 minutes longer when it turned and began to pull cloth with its teeth. (11) Flew directly to cloth after 1 minute. Taken out.

For February 20 the times are: (1) 1¼ minutes; (2) 15 sec-

onds; (3) 2½ minutes. (4) Quiet 12 minutes, was disturbed and then went to the cloth in 2 minutes. (5) Quiet 5 minutes, disturbed, then responded in 1 minute. (6) Quiet 11 minutes; disturbed, then went to cloth in 3 minutes. (7) 45 seconds. (8) 8 seconds. (9) 75 seconds. (10) 45 seconds.

February 21: (1) 75 seconds; (2) 45 seconds; (3) 1½ minutes. (4) Became quiet for 8½ minutes; disturbed, then went to cloth in 1 minute; (5) seven seconds; (6) 12 seconds. (7) Quiet for 5 minutes. Disturbed, then went slowly to cloth in 1 minute. (8) Quiet; disturbed, then became quiet again and was disturbed a second time. Went by indirect route to the cloth 2½ minutes after second disturbance. (9) Ran to front of cage and climbed to cloth in 20 seconds. Dropped the worm given it and then turned around and took hold of the cloth with its teeth. (10) Became quiet; was disturbed after 7 minutes and flew directly to cloth 25 seconds later.

February 22: (1) Put in at 1:57. Flew directly to cloth and pulled at it with teeth in 10 seconds. (2) Flew directly to cloth in 15 seconds. These two trials show that, as on several preceding days, there was no error in finding the cloth. There has been delay due to inhibition of the stimulus or the lethargy of the animal but it has been finding the piece of cloth quickly whenever it was trying to find it.

At this point the bat was taken out of the cage and placed temporarily in a box. The cage was rotated through 180 degrees so that the front now faced the west instead of the east. The observer's chair was also moved to the west side and a box in which there was another bat moving about was moved from the east side where it had been kept during the greater part of the experiments, to the west side. It is to be remembered that the door of the cage is in the middle upper part of the front and the cloth is at the upper, left or back edge of the door, 7 inches from the left end of the cage and 20 inches from the right end.

After the cage was reversed and the observer again seated in front, the bat was placed in it.

Trial (1). — Was placed on the floor facing the cloth; looked about, slowly turning its head, then turned the body and *flew directly to back of cage at a point about 7 inches from the right end*

or the same absolute spot that it had been accustomed to go to, but a place diagonally across the cage from the piece of cloth. Remained there for 7 minutes. (2) Put on floor facing cloth again and looked about, then turned and flew to same point in back in 50 seconds. Seemed to be looking about for cloth, then became quiet. (3) Again put on floor facing cloth, turned and flew to middle of back in 75 seconds and climbed all around over that part of the back of cage. (4) Remained quiet 4 minutes, then turned and flew to same spot as last time; looked and crawled about, then became quiet. (5) Flew to back in 70 seconds and settled down without crawling about. (6) Flew to back in 75 seconds, looked about very little, then became quiet. (7) Put on floor very near cloth, was quiet, then flew directly to back in 60 seconds; climbed and looked around all over back before settling down. (8) Looked around, then turned and flew directly to back, climbed about on back and then became quiet. (9) Remained quietly on floor, then flew to back in 2½ minutes and climbed about over it. Flew to lower right front (possibly attracted by squeakings of another bat in a box near there). Was quiet, then went to back of cage again and climbed about over that; it finally flew to right front corner and from there to the floor where it rested. (10) Flew to back at right of middle and became quiet.

At this point in the experiment the bat was taken out and the cage was turned to its original position. (1) The bat was again placed in the middle of the floor and crossed back and forth several times, then flew to front near cloth in 75 seconds and began pulling at it violently. (2) Flew to cloth in 5 seconds. (3) Flew to cloth in 20 seconds. (4) Flew to cloth in 12 seconds. (5) Flew to cloth in 25 seconds. (6) Remained quiet on the floor, then flew to cloth in 1½ seconds. (7) Flew near cloth and went to it in 30 seconds. (8) Flew near cloth and went to it in 50 seconds.

On the following day the bat was again placed in the cage in its original position, *i. e.*, the front to the east, and on the ten trials of this day it went quickly and without error to the cloth. Before any other experiments could be made with this animal, it escaped from its cage and could not be recaptured.

Four other bats were used in the same kind of experiments between February 7 and March 6. The details of these experiments are, in general, similar to those outlined above. Each of the bats died before the observations were completed.

Bats numbers 4 and 5 both of which were female *Myotis lucifugus*, were used with a piece of bright carmine-red cloth, four by five inches square, in the cage instead of the smaller piece of white cloth. In the case of bat No. 4 the cage was reversed on the second day, or after the animal had been fed at the cloth only 13 times. The association had been quite firmly fixed, however, and the bat went to the back of the cage eight successive times after it had been reversed before it wandered about sufficiently to find the cloth. When it did get to it, it seemed to remember the place and took the cloth in its teeth. It was fed here five times but showed some confusion in finding the place and several times went to the back. The next day it also appeared confused when first placed in the cage and sometimes went to the cloth and sometimes to the back. The following day it seemed to be sick and died two days later.

Results of the Experiments on Association and the Sense of Direction.

These experiments show that visual associations are formed slowly or not at all. Sound associations are formed more readily. Tactile associations were not isolated from others but probably enter into the perceptions which lead to finding the cloth as the animals seemed to have the cloth, as well as the location of it, associated with obtaining food.

The facts relating to the sense of direction will now be taken up. The bats were fed meal worms while they rested on a piece of cloth. The cloth became soaked with the juices of the worms and it also acquired the characteristic odor of the bats to a sufficient degree for the human nose to detect it. The bats did not rely upon the sense of smell for finding the place or they would have reached it without error.

The room in which the experiments were conducted was not as free from noise as might have been desired. However, it was a basement room with thick walls and there was generally no one

except myself in the room or adjoining halls, and outside noises were not heard to a large extent. The only noises recurring with any degree of regularity in the room were those made by the steam in the heating pipes. These could have no direct association with the giving of food while the movements of the observer near at hand did have such an association and these were perceived by several of the animals at times, as when they left the cloth and started toward the sound of the opening door. Therefore sound cannot be considered as a factor in guiding the bats to the back or front of the cage.

Taste and touch may also be counted out, because, if they entered into the food associations at all, they would each tend to guide the animal toward the cloth.

It is not possible to say with so much assurance that sight is not a factor. It was possible for the animals to look through the sides of the cage, but there were no conspicuous objects near and the door of the cage with its latch, and the white or red cloth, were much more noticeable than anything else in sight.

In describing the action of the bat in the cage I have said in a number of places that it "looked around," but it is not certain that this action was really for the purpose of seeing. In a number of trials the animals were so placed that they faced the cloth and if they had been looking for familiar objects as landmarks to guide them to the food they would have noticed it first of all and would have gone directly to it.

The only way in which it seems possible that sight could have aided in their orientation is through the direction of the rays of light. This is not probable because the room was well lighted by windows on two sides and the experimental cage always stood back out of the direct sunlight and also out of the shadows. Moreover, we should not expect to find that animals accustomed to spending all their lives in total darkness or twilight, would depend upon the visual sense for orientation.

While it must be admitted that the experiments did not exclude every possibility of some effective sensations being received through the five senses we commonly know, yet it is not possible to fully account for the behavior of the animals in the experiments above described on the basis of these senses alone, unless

they are developed to a degree which we know nothing about from direct experience.

Watson ('07) found that the ability of white rats to learn a maze was not impaired by the destruction of either the eyes, the olfactory lobes, the middle ear or the vibrissæ, or by anesthetizing the paws or nose, or eliminating temperature and air currents. When the maze was rotated through an angle of 90 degrees, they were confused, but when it was rotated through 180 degrees they were again able to find their way. Watson believes that "static sensations or some non-human modality of sensation" are necessary to explain the behavior of these rats.

Watson and Carr ('08) believe that in the white rats, orientation is attained by traversing a unit of the maze. In man, a train of acts which have become habitual may be set off by some visual or other sensory impulse. In the lower animals such acts may be set off by a "kinæsthetic sensation," such as traversing a unit of the maze and getting the appropriate "feel" of direction from some combination of motor impulses or acts.

Bats are more difficult to work with than rats because their reactions, always uncertain, are seriously disturbed by any kind of operation. Those that I have had have also lacked vitality and have died before extensive experiments could be completed. However, the experiments here described seem to warrant the assumption that they also have something akin to "static sensations" which enables them to retrace their way to a point at which they have been before, without depending on the other five senses.

It is not the purpose of the present paper to discuss the nature of this sense. It may be the same as the "kinæsthetic" sense of Watson. However it is not necessary for a bat to perform an act similar to that of the rats traversing a unit of the maze in order to obtain orientation. The only movements of the bats which seemed to have any connection with orienting was a slow turning of the head in various directions. The purpose of this I could not determine. It is conceivable that if the sense of location is situated in the semicircular canals, a rotation of the head might arouse various sensations, one of which would serve as a clue to position.

There is reason to believe that bats have good memory. On

one occasion a male, *M. lucifugus*, that I had marked by excising the right tragus, escaped through a small crack under the door into another room and thence to the outside through one of several small holes. A few days later I found it in the cave and brought it to the room again, and liberated it.

It circled twice about the room and then dropped to the floor near the door and started directly for the crack and escaped from the house before I had a chance to stop it. Several days later it was recaptured a second time and turned loose in the same room. It started at once for the crack under the door. The crack had now been stopped so that it could not get out, but it ran about in that corner and for several days, whenever liberated in the room it repeatedly went to the place where it had escaped before.

Certain bats, released in a room, show preference for alighting in a particular spot while other individuals select other spots. To illustrate, two bats were allowed to fly about a room lighted by seven windows, all of which received about equally strong light. Each bat alighted a number of times. One of them selected the casing of window number two 12 per cent. of the times and all other windows 12 per cent. Another bat selected window number five 28 per cent. of the times and did not go to window number two at all. Other instances could be cited illustrating the same point. The bats apparently find a place suitable for resting by accident the first time and later return to it because it is remembered.

In experimenting with the bats in the cage, I found that they also learned by accident to find the place where food was to be obtained. When food was once associated with a certain place the animals very quickly learned to go back there. After they once learned the association it remained very persistently. In the experiments with bat No. 2, outlined above, it was so persistent that it prevented finding a new place in ten times the number of trials required the first time.

Memory in all of these cases is doubtless below the realm of consciousness and akin to that which in man is rendered subconscious through habit. Some sort of a memory is absolutely necessary in order to make a sense of direction of any value to

the animal. It is necessary that a bat "remember" the points at which it has been or a sense of direction would not help to orient it.

The sense of direction in these bats may very probably be accounted for, at least in part, by the high development of associative memory. A man can learn to go about a house and make all the turns correctly through habit and with little or no dependence on his senses. In his case it has probably required long experience and many repetitions of the act. In the bats, an act is learned very much more quickly and it is possible that one or two repetitions may even be sufficient to render the performance automatic. If this is true, the ability of the animals to find a place at which they have once been, may be based neither on a sixth sense, nor directly upon any of the five senses, but upon associative memory and quickness in forming habit.

The utility of a sense of direction to bats is so apparent as to scarcely require discussion. It is impossible for sight to be of any service in helping them to find their way in the caves. Outside noises do not go in far and few noises originate there, so that hearing can be of little service in orienting them.

It has been suggested (Blatchley, '96) that air currents may guide them to the mouth of a cave, but this is to me inconceivable. Not only does the direction of the current change in the principal passages but there are always eddies in the chambers and tortuous passages which would tend to confuse rather than help them. The only odors are the constant ones characteristic of a cave and since the bats pass through the air and not along solid surfaces their own odor is not left with a sufficient degree of permanence to be of service in guiding them.

But if a bat have a sense of direction well enough developed to guide it in retracing its way, it would have an immense advantage over other animals of similar habits that lack such a sense. Thus natural selection would foster and improve it.

Conclusions.

Bats are separated from all other mammals by a number of morphological peculiarities which are correlated with the adaptation for flight.

They have no nests, dens or fixed homes. The species studied stay in the caves during the greater part of their existence. They usually go in far enough to be in a constant temperature and total darkness but do not select their resting places with reference to the size of the cave, the nature of the opening or the amount of moisture.

They have few enemies. Consequently fear is but little developed.

About five sixths of a bat's entire existence is spent in a dormant condition. This condition is not dependent upon temperature or season but upon the condition of metabolism; a large amount of fat is favorable to torpor.

In the caves, where conditions of light and temperature are constant, bats come to the cave entrance at irregular intervals. The length of time between these intervals depends upon the amount of surplus fat stored in the body.

They leave the cave only when favorable conditions of light and temperature prevail, and go back to the interior of the cave if the light is too intense or the air too cold.

Food consists of insects that are caught on the wing.

Several senses aid in its perception. Smell and taste are of no use for this purpose. Sight may aid to some extent. Hearing and the tactile sense are chiefly relied on to perceive and locate food.

Bats are more helpless on their feet than most birds. In the air they have greater agility.

They can check their momentum very quickly. In flight, they can secure hold of a surface, only slightly rough, with a single thumb or with one foot.

The breeding habits of our species are not well known. They mate in the fall and the young are born early in the summer. Breeding females leave the caves during the period of gestation and rearing the young.

The sexes do not segregate while they remain in the cave.

Bats in captivity do not readily learn to pick up food from the floor of the cage. They will eat food presented to their mouths and will go to a dish for water.

They do not live well in captivity except when in the quiescent state.

Experimental studies show that neither sight nor the external ears and tragi are necessary for the perception of obstacles during flight.

The body hairs probably have a sensory function.

Obstacles are perceived chiefly through sense organs located in the internal ear.

Perception is probably due to the condensation of the atmosphere between the moving animal and the object it is approaching.

Bats show a remarkable ability to return to a particular spot for food or for the purpose of escaping from an enclosure.

It is difficult to explain how they find their way by means of the five senses familiar to us.

The presence of a sixth sense, that of direction, will explain all of the facts.

It has not been conclusively shown that such a sense exists. If it exists in any animals we should expect to find it in bats. Their habits are such that a sense of direction would be of advantage to them in the struggle for existence.

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